

# AQUATIC ADAPTATIONS OF THE WATER MOUSE, *RHEOMYS UNDERWOODI*

By ANDREW STARRETT AND GEORGE F. FISLER<sup>1</sup>

**ABSTRACT:** An adult male *Rheomys underwoodi* caught alive along the Río Poasito, at 2000 m on Volcán Poás, Alajuela Province, Costa Rica, in April, 1966, was maintained in captivity for a short time. Limited observations on maintenance behavior and locomotion of this animal are presented. In addition, morphological features (body form, tail shape and foot structure) related to the high degree of specialization for aquatic locomotion shown by this rodent are described, and some ideas concerning the evolution of the semi-aquatic habit are discussed in relation to *Rheomys* and other small mammals.

## INTRODUCTION

Information available on the biology of the genus *Rheomys* is quite limited. These animals live primarily in and around swift flowing streams of the Neotropics. Howell (1930) described certain aquatic features of *Rheomys* but did not give a full account of the high degree of adaptation to a semi-aquatic existence which the species *R. underwoodi*, in particular, exhibits. Hooper (1968) briefly mentioned some of the aquatic characteristics of *Rheomys* in a comparison of *R. underwoodi* and *R. hartmanni*, the two species which occur in Costa Rica, and also included ecological information and stomach analyses for both. Our capture of a living animal has prompted us to record some observations on the behavior and morphology of the water mouse with additional comments on aquatic adaptations in this and other species.

On the basis of information and materials provided for us by Emmet T. Hooper, we set 31 traps (18 museum specials, 13 National single door live traps) along the banks of the Río Poasito, 2000 m, Volcán Poás, in Alajuela Province, Costa Rica, on the evening of 9 April 1966. This same area was trapped on 6 and 7 April 1966 by Hooper and James H. Brown and is described by Hooper (1968). Instead of using the method of trapping *Rheomys* described by Stirton (1944), we set seven live traps along relatively quiet eddy pools just outside white-water areas. Our *Rheomys* was taken near such a pool in a trap which was placed on rocks about 7.5 cm above the water line. The mouth of the trap was about 20 cm from the pool, one meter from any white water, and 15-20 meters below a small waterfall. Bait used was peanut butter with sardine meat and oil spread over it, placed on the treadle inside of the trap. Some sardine oil was smeared on the trap entrance but no bait was placed outside of the trap. No other mammals were taken in the live traps

<sup>1</sup>Both authors: Research Associates, Los Angeles County Museum of Natural History; and Department of Biology, San Fernando Valley State College, Northridge, California 91324.

but three *Reithrodontomys creper* and one *Peromyscus nudipes* were caught in the snap traps. About half of the snap traps were placed next to the water. The water mouse was an adult male having abdominal testes (10 x 18 mm) with epididymides well developed and caudae protruding into the inguinal passages. The standard measurements are 300-158-39-7 (mm).

#### GENERAL BEHAVIOR

The actions of the *Rheomys* when first observed were slow and deliberate, as if it had been in the trap for some time and was weakened, but later it became more active. It darted about the trap hurriedly, in the manner of a shrew, yet when quiet, it sat mostly hunched over like a muskrat (*Ondatra zibethicus*). Stirton (1944) described it as a miniature model of a beaver (*Castor canadensis*). When seated, its hind feet were spread out at an angle of some 30-40 degrees from the body with its fore feet usually tucked along its chest. A striking, and probably adaptively significant reaction, was its tendency to bite at objects with which it came into contact. Even while being carried in the trap, it nipped at fingers whenever it encountered them at the edges of the trap as it dashed about. When handled, however, it was docile and did not bite, and attempts to induce it to nibble fingers were successful only if the animal blundered into them, as it did not seem to seek out such prey. The biting reaction on contact with moving objects was also later shown when the animal was observed swimming. In the capture of prey under water, where vision and olfaction may be of minimal use, it would be of great advantage for an animal to be adapted to biting at any moving object with which it came in contact. The eyes of this rodent are very small and presumably are of little use, particularly under water, and especially in fast moving, turbulent streams. The face is rather well endowed with vibrissae, probably advantageous in hunting and orientation, but it was difficult to tell if they were used as sensors.

When the trap was first observed, all of the bait had been eaten, or, less likely, washed away. Our captive animal was fed small pieces of sardines which it ate from the container rather than manipulating the food while sitting up as do many of the more familiar rodents. It occasionally manipulated larger chunks of sardine (10-12 mm) with its fore feet, so perhaps the size and consistency of the food determines the manner of feeding. It probably handles insect larvae with its fore feet. In general, the animal would eat for a minute or so, pause for 15-20 seconds, and then resume eating. It was first fed about thirty minutes after the trap was picked up and it ate roughly a small thimbleful of sardines in the succeeding hour. Attempts at feeding it green vegetation (leaves and herbs from its habitat) while it was still hungry were unsuccessful. Stirton (1944) found no evidence that *Rheomys* was piscivorous but thought that it was omnivorous and even cannibalistic. Goldman (1920) suggested that one species may feed on snails. Hooper's (1968) analysis of contents from six stomachs of *Rheomys* from Costa Rica and Guatemala (one stomach

empty) shows a diet of primarily aquatic insect larvae. Fish are present in the Río Poasito but are not native. Our captive was observed drinking sparingly. It lapped with its tongue in the familiar manner of many small rodents, directly off the water surface.

When first seen in the trap, the *Rheomys* was dry except for its tail, underparts, feet and muzzle. After removal from the stream area, it dried quickly. Grooming was accomplished in the manner of many rodents, except that the enlarged hind feet serve as very effective combs for the body fur. When wet or grooming, or both, as grooming is evidently an important part of the drying process, the animal moved the skin of the back in a peculiar fashion, appearing to erect the guard hairs, a grooming as well as a drying aid. This movement appeared to pass in waves over the hunched back antero-posteriorly and the reverse. All of the time the animal sat much like a muskrat. After leaving the water, the animal groomed extensively.

Limited swimming observations of the captive *Rheomys* were made in a small 27 x 36 cm wash basin. The water was about 8 cm deep and for part of the time the trap was used as an island although the basin could barely accommodate it. The small size of the container restricted the movement of the animal. It tried to climb the sides, violently treading water with its hind feet, maintaining its body about half to two-thirds out of the water. The large hind feet made tremendous splashes as it attempted to escape, very strikingly pointing out their propulsive power. Observations of diving were limited but the process was extremely quick. While swimming on the surface, the mouse had its head out of the water, the rump under, while the tail was curved concavely with the tip at the water surface. Most of the swimming motion was with the hind feet with little body undulation except when sculling (noted only 2 or 3 times). These latter motions seemed to give the animal added impetus for quick acceleration or turning. The fore feet could not be seen while swimming, indicating that they are not used other than to hold on to objects when landing, or perhaps to fend off objects while swimming. In all swimming motions, the animal was extremely quick, presumably an adaptive feature for feeding under water as well as for swimming in swift moving streams. Hooper (1968) has reported on the swiftness in movement and swimming of an animal, undoubtedly *Rheomys underwoodi*, observed in the wild.

While in captivity, the animal lived in the trap. Soft tissue and newspaper given to the *Rheomys* was slightly shredded but no real nest building occurred. Excelsior was ignored. Rather, the animal slept mostly on its side rolled in the typical rodent ball, under the paper. Stirton (1944) mentioned that water mice probably nest in dead brush and logs lodged in the stream or under large boulders or other rocks.

After the swimming session on the evening of capture, the animal appeared to be drying rather slowly. However, by the following morning (11 April) it was dry and appeared to be in good health. It ate readily (sardines). It was placed in a light cloth sack for transport to Los Angeles, California,

but it died in transit. The specimen was preserved as a skin and skull with the body preserved in fluid and is now in the collection of the Los Angeles County Museum of Natural History (LACM 28260).

#### MORPHOLOGY

Because of the absence of such information from the literature, and in order to lay the background for a discussion of the adaptations of this animal to a semi-aquatic existence, a detailed account of pertinent morphological characters is here provided. The body is streamlined to a high degree with essentially no projections other than the hind feet and tail when in the water. The head is somewhat depressed and the mouth opening is small. The eyes are also reduced in size. The snout is truncated in dorsal view and the rhinarium is prominent. The nostrils are situated laterally and open posteriorly behind flaplike valves. The numerous vibrissae are situated dorsally and laterally on the snout and cheeks posterior to the rhinarium and around the mouth. They reach maximum lengths of 32 to 34 mm, although most are 14 to 26 mm long. The ear pinnae are reduced essentially to small, pointed posterior lobes, about 4 mm in length, which do not extend above the surface of the fur.

The pelage is generally dense and soft, the type characteristically associated with the smaller aquatic mammals. In the mid-dorsal region the underfur is dense with fine hairs which range from 5 to 7 mm in length. Abundant but less dense and grosser hairs, about 12 to 14 mm long, form an outer layer. The ventral pelage is similar to that of the dorsum, but the underfur is shorter.

The fore limbs are relatively short and do not project much from the body, even when walking. The proximal portions of the hind limbs blend similarly into the body contours, leaving the remarkable hind feet as the only limb segments which project obviously from the furred outline of the body. The tail also is flared into the body outline over the proximal 15 mm of its length. The front feet are much smaller than the hind feet with long, curved, sharply pointed claws. On the hind feet, digit I is the shortest, then in order of increasing length, digits V, II, III, and IV. The greatest differences in length are between digits I and II and, to a lesser degree, between digits V and IV. The first and, to a lesser extent, the fifth digits appear to have the greatest amount of independent movement.

The hind feet have laterally compressed digits interconnected by webbing. The sides of the feet and toes are lined with single rows of closely spaced stiff hairs which reach maximum lengths of three and four mm on the medial and lateral sides of the feet, respectively, and two to three mm on the toes and webbing, with the shortest hairs being those near the middle of each web. The claws are deep and essentially as broad as the tip of the terminal phalanx, that on digit I being the deepest and the claw on digit II the broadest. The tips are pointed in lateral profile, but somewhat rounded and scooplike in ventral aspect. The massive appearance of the hind claws is very striking when they



are compared with those of other rodents of similar size such as *Neotoma*, *Nelsonia*, *Xenomys*, *Tylomys*, *Nyctomys*, and *Rattus*.

When the digits are abducted, the webbing reaches the level of the pennultimate interphalangeal joint between digits II, III, IV, and V, but is less extensive between digits I and II. Each web originates at the base of the claw and extends, as a widening flap, to the levels just mentioned. There the margin turns and a similar but narrower flap continues to about the same claw level on the next toe. On the lateral (post-axial) side of each digit, the webbing arises along the dorsolateral surface, whereas on the medial side of the succeeding digit it connects along the medial surface. When the foot is extended, the digits rotate so that their ventral surfaces turn mediad. The metatarsophalangeal joints are somewhat loose, apparently allowing the digits to rotate even more than do the metatarsals. The metatarsals (except III and IV) and free digits abduct and, since they are rotated, the latter also extend at the metatarsophalangeal joints in a more or less horizontal plane. These actions spread the foot and toes while turning the digits so that they present their broad compressed surfaces and spread the webbing to its greatest extent. Part of the rotation of the digits may be passively effected by the tension of the webbing.

When fully expanded, the hind foot of our specimen measured 14 mm across the plantar surface at the level of the distal ends of the metatarsals, and the expanded hair fringes added another six mm at that level, resulting in greatest dimensions of 20 x 39 mm. Planimetric measurements of the best of a number of inkpad prints of the right hind foot, including hair fringes, showed areas of 3.8 to 4.0 cm<sup>2</sup>. The two hind feet, then, form impressive propulsive surfaces during extension in the backward stroke while swimming. In the recovery stroke, it is probable that the foot is flexed and the digits flexed, abducted, and possibly rotated somewhat laterad again so that the compressed toes are curled slightly and lie close together in a staggered sequence (cross sectional), with digit I leading, and the hair fringes flattened against the sides of the foot and toes. Thus the pes becomes narrowed with the digit alignment presenting a laterally compressed, rather than an anteroposteriorly flattened unit, approaching the characteristics of a hydrofoil, and offering minimum resistance to the water.

The free tail, from the point at which it leaves the furred base which flares into the body, measures 143 mm to the tip. The proximal 30 mm is circular in cross section and approximately 7 mm in diameter. At the end of this basal portion, there is a constriction to about 6.5 mm diameter and the tail gradually tapers and becomes compressed. In the last 15 mm the tail narrows more rapidly to almost a point in dorsal view and, in lateral aspect, reaches its shallowest dimension (a little less than 5 mm), then expands slightly ventrally and ends in a somewhat rounded tip which gives the appearance of turning a little ventrad. Along the ventral surface of the free tail, particularly from the level of the basal constriction where the cross section of the tail begins to change shape, the hairs arising from the ventral surface of the tail, representing approximately  $\frac{1}{3}$  the tail circumference arc, become abruptly longer (to

about 5 mm) and more dense, forming a kind of broad fringe extending along the undersurface of the tail to the point where it expands ventrally near the tip. The hairs on the rest of the free tail are shorter and relatively sparsely but evenly distributed. Internally the most notable feature of the tail structure is the presence of numerous heavy tendons attaching firmly to the vertebrae, fascia and skin, distal to the basal constriction. The extraction of the tail beyond this point during skinning was difficult. (James H. Brown, personal communication, recalled the same difficulty with the specimens of *R. underwoodi* he prepared from the same locality.) This clearly suggests well developed muscular control of the tail, further evidence of which was obtained by selective pulling of the tendons, while the tail was partially extracted, which caused bending in various directions and at different points in the more distal portions of the tail.

The streamlining provided by reduction and blending of projecting parts of the body and the generally fusiform shape and flared tail base make *Rheomys* a hydrodynamically efficient body. The large hind feet provide the main propulsive force and in recovery strokes tend to give minimum resistance by the combined characters of compressed digits and the foot action mechanism. The tail apparently serves a stabilizing and a supplementary propulsive function, being adapted for both by compression, by effective control through the tendon arrangement, and probably also by the paddle-shaped tip. Dorsal-ventral bending of the tail was noted above, during surface swimming. The slightly ventrally oriented distal portion of the tail (the paddle) probably is significant when the tail is thus curved in such a way that the tip approaches, or is at, the water surface while the rest of the tail is below. The tip then would be more nearly horizontally oriented. This curving might also make the ventral hair fringe stand out more and so contribute to the compressed tail shape. This fringe may serve other functions since the hairs are not particularly stiff. Possibly it protects the ventral surface of the tail from abrasion by streamside rocks and gravel, or it may serve as a drip line for rapid water runoff.

The thoracic vertebrae of the skinned carcass were capable of rather acute kyphotic curvature. The panniculus carnosus is a rather broad, thin sheet posteriorly (lumbosacral region), but gives rise to a number of long, narrow extensions running up over the back to the head and shoulder region. Contraction of this muscle pulls the skin back and forth over the thoracic region. This action separates the hairs of the back when the thoracic region is curved during grooming.

#### DISCUSSION

In attempting to understand aquatic adaptation of *Rheomys underwoodi*, we surveyed certain literature on semi-aquatic mammals. (Anthony, 1921, 1923, 1929; Bauchot and Stephan, 1968; Conaway, 1960; Dickey, 1928; Enders, 1938; Goldman, 1912, 1920; Goodwin, 1959; Guth *et al.*, 1959; Handley and Mondolfi, 1963; Hershkovitz, 1944, 1955; Hooper, 1947, 1968; Howell, 1930; Lönnberg, 1921; Malzy, 1965; Peyre, 1956; Stirton, 1944;

Svihla, 1934; Thomas, 1893, 1897, 1906a, 1906b, 1924a, 1924b; De Winton, 1896). Most of our comparative information was taken from Walker (1968). Although the survey was not exhaustive, we found that relatively little is known about semi-aquatic small mammals, especially the more highly specialized forms. However, limited discussion of the position which *R. underwoodi* occupies in the evolution of specializations in these mammals is possible.

*Rheomys underwoodi* is among the most highly hydrodynamically specialized mammals, particularly when compared with species of comparable size and habits, the smaller semi-aquatic rodents and insectivores, and the marsupial *Chironectes*. On the basis of what we could determine, it is quite likely that most aquatic features of *R. underwoodi* are not unique, but a comparable total combination of specific features is apparently limited to members of only eight other genera: three of rodents (in addition to certain other *Rheomys* species), *Anotomys*, *Ichthyomys* (both closely related to *Rheomys*), and the hydromyine *Crossomys*; five of insectivores, *Limnogale*, and *Micropotamogale* (*M. ruwenzori*) (Tenrecidae), *Desmana* and *Galemys* (Talpidae) and *Nectogale* (Soricidae). As might be expected, the details of specialization are most similar among the rodents. *Limnogale* and *Nectogale* seem to be the most closely comparable of the insectivores.

Davis (1964:323) considered two factors to be "primarily responsible for adaptive modifications in the morphology of mammals: locomotion, and foods and feeding." In the case of forms which are more highly adapted for aquatic living, the locomotor requirements strongly influence the morphological modification related to obtaining food. In those particularly adapted for rapid swimming, morphological feeding specializations not in accord with the hydrodynamic requirements imposed by locomotor specializations are not to be found. Although this applies to semi-aquatic, or amphibious mammals, as well as to the more completely aquatic, the degree of overall modification in the former is limited by the requirements of terrestrial locomotion, and a structural-functional balance is struck according to the relative significances of aquatic and terrestrial locomotion in the lives of these animals. Furthermore, not all aquatic adaptations contribute directly to aquatic locomotion, and the ability to swim does not necessarily involve much in the way of morphological modification (Howell, 1930). *Rheomys underwoodi* must be considered a semi-aquatic rodent with a high degree of morphological specialization reflecting primarily selection for effective, rapid aquatic locomotion as the major influence.

Davis (1964:323) further stated that "In mammals the major forces impinging on locomotion are escape from enemies, pursuit of prey and wandering in search of food or water." These categories can be modified to include as potentially significant functions (forces or factors): 1) simple translocation or unforced movement (wandering for whatever reason); 2) escape from predators; 3) escape in the event of changing environmental conditions; 4) locating and feeding on plants (or mollusks; *i.e.* stationary food); 5) pursuing and capturing other animals (mobile food). All of these can play a part



in determining the degree of adaptation for aquatic locomotion in the evolution of semi-aquatic forms. One other important factor remains which has a basic influence on the selective requirements related to the five functions just listed: namely, the nature of the aquatic environment. Ability to swim in still water requires less in the way of morphological specialization than does the ability to swim in a strong current (function 1 or 4 above), and if forced locomotion (functions 2 and 5) is required, then increased specialization becomes a necessity under both types of aquatic conditions. Escape by swimming from predators that do not swim puts more stress on the ability to get into the water rapidly than it does on swimming. The high degree of hydrodynamic specialization in *Rheomys underwoodi* appears to have evolved as an adaptation of this semi-aquatic rodent for unforced movement, escape from predators and, probably most significantly, for obtaining moving food in the sometimes torrential streams along which it lives. The adaptive features related to these factors doubtless have survival value, as well, when the streams rise rapidly and become swifter and more turbulent during heavy rains (function 3).

The types of food (discussed in more detail by Bauchot and Stephan, 1968) and the type of aquatic environment appear to be the most important factors in the evolution of the semi-aquatic radiation among small mammals. Most semi-aquatic herbivorous mammals occur in level or lowland and coastal regions in which graminoid and low herbaceous vegetation forms a major source of food and where marshes, ponds and river overflows are to be found but rapid streams are unusual. In such situations, water edge species probably took to water, mainly, in order to take advantage of the additional (similar) plant food thus made available and also to survive during periods of flooding. In this category apparently fall most of the semi-aquatic rodents, of which many are little specialized aquatically; others show varying degrees of specialization, but all are still limited by the importance of terrestrial locomotion as a means of dispersal and of relocation during times of change in their aquatic habitats.

Among those showing little or no specific adaptations for aquatic locomotion, but which more or less routinely enter water and swim, can be mentioned species of *Thryonomys* (Thryonomyidae), *Bandicota*, *Dasymys*, *Hybomys* (Muridae), *Microtus*, *Oryzomys* and *Reithrodontomys* (Cricetidae), to name only a few in just these three families (see Walker, 1968; Fisler, 1961, 1965). Species of other genera have evolved definite aquatic locomotor specializations and apparently utilize more of the food occurring in the water: the oryzomine *Nectomys*, the sigmodont *Holochilus*, and the microtine *Arvicola* are obvious examples. Those genera (such as *Hydrochoerus*, *Myocastor*, *Ondatra*, and *Neofiber*), which have become more dependent on semi-aquatic or aquatic plant food, have evolved more aquatic locomotor specializations and are capable of swimming in relatively slow and steady currents present in small streams and rivers. It seems significant that these last mentioned genera are among the larger rodents, suggesting that there is a relationship between



the size of the animal and the ability to enter larger bodies of water and stronger currents where more sustained swimming is required. As must be the case with all aquatic and semi-aquatic mammals, their respective degrees of specialization have evolved in relation to the most severe aquatic conditions (currents, distances to be covered in water) in the bodies of water which they frequent or inhabit. Many of the rodents mentioned may be found in a variety of aquatic situations, but few, if any, characteristically occur in water with rapid currents. None feeds to any extent on active aquatic food although some do utilize inactive aquatic animals at least occasionally. The water opossum, *Chironectes*, seems to be comparable with this group of rodents in terms of degree of aquatic specialization, but it also fits in with the next group of small mammals in that it both feeds on aquatic animals and probably evolved in a forest environment.

Apparently the semi-aquatic insectivores and the more highly specialized semi-aquatic rodents have evolved, for the most part, in hilly or mountainous regions. Here forest is more prevalent than open grassland or other vegetational types which provide much in the way of leafy food, and moving water characterizes the aquatic habitats (streams and small rivers). Some of these conditions, and/or other coincident factors, have apparently been favorable to insectivore radiations, and the presence of good sources of food along the water edge and in the water itself has provided the setting for the evolution of the semi-aquatic members of the order. The more highly specialized insectivores already mentioned are characteristically found associated with streams or small rivers, usually in forested areas. The other known semi-aquatic insectivores show somewhat wider and more variable ecological characteristics but probably have evolved under similar conditions. *Potamogale*, one of the largest insectivores, is unique among semi-aquatic members of the order in having a highly specialized tail as its sole locomotor organ, a feature which probably makes it one of the most efficient swimmers of the group (more nearly comparable to the otters). This African tenrecid is found in all types of water, from lakes to torrential mountain streams. The remaining semi-aquatic members of this order are not highly specialized for aquatic locomotion showing only relatively slight modifications of the terrestrial locomotor apparatus. They do not possess swimming abilities comparable to those of the insectivores already mentioned. The relatively large hind feet, long tail and more streamlined body of the star-nosed mole, *Condylura*, (as compared to typical moles) are of positive value in aquatic locomotion, if not direct specializations for this function, as well may be the less fossorially modified fore limb of this animal. The water shrews belonging to the soricid genera *Neomys* and *Chimarrogale* and species *Sorex palustris* and *S. bendirii* probably can be considered ecological equivalents (roughly) in their respective separate ranges of distribution, having approximately the same morphological adaptations (fringed feet and tail). They appear to be most similar in aquatic adaptations to the less specialized species of the Neotropical rodent genera *Holochilus* and *Nectomys*. Finally, *Micropotamogale lamottei*, characteristically found in

slower waters, seems to be morphologically adapted for aquatic locomotion to about the same extent as the water shrews although it is larger and shows more aquatic specializations.

The insectivores mentioned previously as being adaptively comparable to *Rheomys underwoodi* are more highly specialized for aquatic locomotion and are, in fact, more aquatic than those just discussed, with the exception of *Potamogale*, and they characteristically live in rivers and rapid to torrential streams. Their adaptations have evolved in response to the requirements imposed by more or less active pursuit of food in the currents and turbulence of the aquatic environment.

In comparison with this last group of insectivores, rodents living in regions characterized by forested streams and rivers have less potential food available in and around the water if they depend on plant sources. Those entering the streams have had to assume a diet of moving animal food (most likely before taking to the water), the capturing of which, under the aquatic conditions presented by the active waters, has been a significant factor in the evolution of their locomotor specializations. Two groups of rodents have shown somewhat similar radiations in such situations: the Neotropical ichthyomyine cricetids and the New Guinea-Australian hydromyine murids.

The ten genera of hydromyines (with some 16 species) are diversified and include small mouse and shrew-like forms (*Microhydromys*, *Parahydromys*) and other apparently terrestrial herbivores, as well as three genera which have taken to the water and include animals in their diets. These three, *Xeromys*, *Hydromys* and *Crossomys*, have followed different lines of specialization representing the extremes of the spectrum of aquatic modifications found in other groups of rodents (Lidicker, 1968; Mahoney, 1968; Tate, 1951). *Xeromys*, the only endemic Australian genus of hydromyines, feeds on aquatic vegetation and inactive aquatic mollusks in swampy situations and has little, if any, apparent morphological adaptations for aquatic locomotion. The more widely distributed genus, *Hydromys*, represents a more muskrat-like type of semi-aquatic specialization, with the widespread *H. chrysogaster* being associated with a wide range of aquatic environments and feeding on a variety of animal and plant foods. Finally, the monotypic New Guinean genus *Crossomys*, found along mountain streams and very likely feeding on aquatic animals, appears to be most similar to *Rheomys underwoodi* in ecological characteristics and in both degree and detail of morphological adaptation for aquatic locomotion.

The five genera of ichthyomyines are less diversified than the hydromyines, rather they show differing degrees of specialization for life along mountain streams. Hershkovitz (1962) proposes that the ichthyomyines are derived from pastoral forms, primarily on the basis of dentition; we believe that, in any case, the ancestral forms most likely had to enter the forest to be exposed to the stream habitat, since gallery forest, at least, is almost always associated with permanent streams in the New World Tropics. The monotypic genera *Neusticomys* and *Daptomys* exhibit only slight morphological modifi-

cation for aquatic habits, whereas the various species (16 named forms; eight to 14 species, depending on the authority consulted) of *Rheomys* and *Ichthyomys* carry aquatic locomotor modifications to varying extents of specialization (Cabrera, 1961; Goodwin, 1959; Handley and Mondolfi, 1963; Hooper, 1968). *Anotomys* (monotypic), *Rheomys underwoodi*, probably *R. mexicanus* (according to the informative description provided by Goodwin, 1959) and several other species of *Rheomys* (Hooper, 1968) and of *Ichthyomys* (Anthony, 1929) appear to have attained more or less similar high levels of aquatic locomotor adaptation, along several parallel evolutionary pathways. As already pointed out by Hooper (1968), the other ichthyomyine species found in Costa Rica, *Rheomys hartmanni*, shows less specialization for aquatic locomotion than does *R. underwoodi*. The LACM specimen of *R. hartmanni* (LACM 25418) from north of San Isidro del General, in the Cordillera de Talamanca (Hooper's 5200-ft. station, Río Buena Vista tributaries, Prov. San José; Hooper, 1968) shows the lesser degree of specialization of the fur, ears, hind feet and tail indicated by Hooper (1968) and, furthermore, shows much less (negligible) webbing of the hind feet, and a tail which appears to be round and to lack the ventral hair fringe. This specimen also lacked the specialized tail muscle-tendon complex described above in *R. underwoodi*.

Differences such as those between *Rheomys underwoodi* and *R. hartmanni*, which have been outlined, are not always readily explainable. A more thorough interpretation of the evolution of the adaptations of small mammals to the semi-aquatic habit awaits a detailed knowledge of these adaptations. Most references we have seen have been taxonomic in nature and have discussed mainly diagnostic or comparative features of the mammals described, presenting little useful information on other aspects of their morphology. More ecological data, such as kinds of food consumed and detailed characteristics of habitats where the animals are found, along with information on behavioral adaptations, will provide bases for interpreting the significance of morphological specializations.

#### ACKNOWLEDGMENTS

The LACM specimens and original field data reported in this paper were collected in 1963 and 1966 during work carried on in Costa Rica as part of the Los Angeles County Museum of Natural History mammalian ectoparasite project (LACM-USACR; see Starrett and Casebeer, 1968) under U.S. Army Medical Research and Development Command grants No. DA-MD-49-183-62-G54 and DA-MD-49-193-63-G94 (F. S. Truxal and C. A. McLaughlin, Jr., principal investigators). It should also be mentioned that both LACM specimens of *Rheomys* were previously recorded in relation to this project by Geest and Loomis (1968). In addition, in 1966, facilities and various services were provided by The Organization for Tropical Studies (O.T.S.) and the Universidad de Costa Rica, San José. The authors wish to thank, in particular, Norman J. Scott, Jr., O.T.S., for his help. We also here express our appreciation to Emmet T. Hooper and James H. Brown for their invaluable courtesy in loaning traps to us and providing information and advice on several occasions.

## RESUMEN

Un macho adulto de *Rheomys underwoodi* fué capturado vivo, en Abril, 1966, en la orilla del Río Poasito, a 2000 m en el Volcán Poás, Provincia de Alajuela, Costa Rica. En captividad, éste animal comió sardinas de lata vorazmente, pero reusó varios tipos de plantas de la región de captura que le fueron ofrecidas. En general, sus acciones al moverse en la trampa, como limpiandose y comiendo, fueron rápidas y parecidas a las acciones de musarañas. Basado en observaciones limitadas de éste roedor semi-acuático en el agua de un recipiente restringido, su comportamiento mostró tambien acciones rápidas al entrar y salir del agua, nadando en la superficie o zambullendose. La propulsión era efectuada por movimientos alternados de las anchas patas traseras.

Entre las especializaciones morfológicas adaptadas a la locomoción acuática, que éste ratón presenta, las siguientes han sido notadas: un cuerpo hidrodinámico del cual solo las patas traseras y la cola protruden durante la natación, la cola ligeramente compresada longitudinalmente con arreglo complejo de tendones para su control; piés traseros grandes con tela interdigital y crestas de pelos que dan una superficie total de cada pié de aproximadamente 3.9 cm<sup>2</sup>. Además, las patas traseras pueden voltear y doblarse de tal manera que presentan una estructura de "hydrofoil," con una resistencia mínima contra el agua durante el movimiento hacia adelante (de recobro) al nadar.

Finalmente, en una forma general y especulativa, una discusión de la evolución de hábitos semi-acuáticos en pequeños mamíferos es presentada. Dos cursos principales se pueden proponer: 1) en áreas de tierras bajas, donde el habitat acuático consiste principalmente de aguas quietas o lentamente corredizas y la vegetación acuática es abundante, los pequeños mamíferos semi-acuáticos son en su mayoría roedores que comen, principalmente, plantas, y que tienen tendencia a producir especializaciones morfológicas limitadas para locomoción acuática; 2) en áreas de montaña bien forestadas, donde los arroyos y riachuelos tienen aguas rápidas que contienen más animales acuáticos que plantas acuáticas, los hábitos semi-acuáticos se han desarrollado en varios insectívoros y algunos grupos de roedores que han podido adaptarse a una dieta de pequeños animales. *Rheomys underwoodi*, así como otros roedores ichthyomyiines Neotropicales y los roedores hydromyines, *Crossomys*, de Nueva Guinea, pertenecen al último grupo y han desarrollado un alto grado de especialización morfológica a la locomoción en aguas rápidas, a veces torrentosas, en que ellos viven.



## LITERATURE CITED

- ANTHONY, H. E. 1921. Preliminary report on Ecuadorean mammals. No. 1. Amer. Mus. Nov., 20: 1-6.
- . 1923. Preliminary report on Ecuadorean mammals. No. 3. Amer. Mus. Nov., 55: 1-14.
- . 1929. Two new genera of rodents from South America. Amer. Mus. Nov., 383: 1-6.
- BAUCHOT, ROLAND, AND HEINZ STEPHAN. 1968. Etude des modifications encephaliques observées chez les insectivores adaptés a la recherche de nourriture en milieu aquatique. Mammalia, 32: 228-275.
- CABRERA, A. 1961. Catalogo de los mamíferos de America del Sur. II. Buenos Aires, Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," Rev., Cienc. Zool., 4: 309-732.
- CONAWAY, C. H. 1960. The water walker. Nat. Hist., 69(6): 21-25.
- DAVIS, D. DWIGHT. 1964. The giant panda, a morphological study of evolutionary mechanisms. Fieldiana: Zool. Mem., 3: 1-339.
- DE WINTON, W. E. 1896. On some mammals from Ecuador. Zool. Soc. Lond., Proc., pp. 507-513.
- DICKEY, DONALD R. 1928. Five new mammals of the rodent genera *Sciurus*, *Orthogeomys*, *Heteromys*, and *Rheomys*, from El Salvador. Biol. Soc. Wash., Proc., 41: 7-14.
- ENDERS, ROBERT K. 1938. A new rodent of the genus *Rheomys* from Chiriquí. Acad. Nat. Sci. Phila., Proc., 90: 295-296.
- FISLER, GEORGE F. 1961. Behavior of salt-marsh *Microtus* during winter high tides. J. Mammal., 42: 37-43.
- . 1965. Adaptations and speciation in harvest mice of the marshes of San Francisco Bay. Univ. Calif. Publ. Zool., 77: 1-108.
- GEEST, JULIUS C., AND RICHARD B. LOOMIS. 1968. Chiggers of the genus *Pseudo-schoengastia* (Acarina: Trombiculidae) from Costa Rica. Los Angeles Co. Mus. Nat. Hist., Contrib. Sci., 150: 1-49.
- GOLDMAN, EDWARD A. 1912. New mammals from eastern Panama. Smiths. Misc. Coll., 60 (2): 1-18.
- . 1920. Mammals of Panama. Smiths. Misc. Coll., 69(5): 1-309.
- GOODWIN, GEORGE G. 1959. Descriptions of some new mammals. Amer. Mus. Nov., 1967: 1-8.
- GUTH, C., H. HEIM DE BALSAC, AND M. LAMOTTE. 1959. Recherches sur la morphologie de *Micropotamogale lamottei* et l'évolution des *Potamogalinae*. I. Ecologie, denture, anatomie crânienne. Mammalia, 23: 423-447.
- HANDLEY, CHARLES O., JR., AND EDGARDO MONDOLFI. 1963. A new species of fish-eating rat, *Ichthyomys*, from Venezuela (Rodentia Cricetidae). Acta Biol. Venezuelica, 3: 417-419.
- HERSHKOVITZ, PHILIP. 1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Univ. Mich., Mus. Zool., Misc. Publ., 58: 1-101.
- . 1955. South American marsh rats, genus *Holochilus*, with a summary of sigmodont rodents. Fieldiana: Zool., 37: 639-688.

- . 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the Phyllotine group. *Fieldiana: Zool.*, 46: 1-524.
- HOOPER, EMMET T. 1947. Notes on Mexican mammals. *J. Mammal.*, 28: 40-57.
- . 1968. Habitats and food of amphibious mice of the genus *Rheomys*. *J. Mammal.*, 49: 550-553.
- HOWELL, A. BRAZIER. 1930. Aquatic mammals. Chas. C. Thomas, Baltimore 338 p.
- LIDICKER, W. Z., JR. 1968. A phylogeny of New Guinea rodent genera based on phallic morphology. *J. Mammal.*, 49: 609-643.
- LÖNNBERG, EINAR. 1921. A second contribution to the mammalogy of Ecuador, with some remarks on *Caenolestes*. *Ark. for Zool.*, 14(4): 1-104.
- MAHONEY, J. A. 1968. *Baiyankamys* Hinton, 1943 (*Muridae*, *Hydromyinae*) a New Guinea rodent genus named for an incorrectly associated skin and skull (*Hydromyinae*, *Hydromys*) and mandible (*Murinae*, *Rattus*). *Mammalia*, 32: 64-71.
- MALZY, P. 1965. Un mammifère aquatique de Madagascar: le limnogale. *Mammalia*, 29: 400-411.
- PEYRE, A. 1956. Ecologie et biogéographie du desman (*Galemys pyrenaicus* G.) dans les Pyrénées françaises. *Mammalia*, 20: 405-418.
- STARRETT, ANDREW, AND RICHARD S. CASEBEER. 1968. Records of bats from Costa Rica. Los Angeles Co. Mus. Nat. Hist., Contrib. Sci., 148: 1-21.
- STIRTON, R. A. 1944. Tropical mammal trapping I: the water mouse *Rheomys*. *J. Mammal.*, 25: 337-343.
- SVIHLA, ARTHUR. 1934. The mountain water shrew. *Murrelet*, 15: 44-45.
- TATE, G. H. H. 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Amer. Mus. Nat. Hist., Bull.*, 97: 183-430.
- THOMAS, OLDFIELD. 1893. On some mammals from central Peru. *Zool. Soc. Lond., Proc.*, pp. 333-341.
- . 1897. Descriptions of four new South-American mammals. *Ann. Mag. Nat. Hist.*, (6) 20: 218-221.
- . 1906a. A new aquatic genus of Muridae discovered by Consul L. Soderström in Ecuador. *Ann. Mag. Nat. Hist.*, (7) 17: 86-88.
- . 1906b. A third genus of the *Ichthyomys* group. *Ann. Mag. Nat. Hist.*, (7) 17: 421-423.
- . 1924a. On a new fish-eating rat from Bogotá. *Ann. Mag. Nat. Hist.* (9) 13: 164-165.
- . 1924b. A new fish-eating rat from Ecuador. *Ann. Mag. Nat. Hist.* (9) 13: 541-542.
- WALKER, ERNEST P. 1968. *Mammals of the World*. 2nd Ed., rev. (John L. Paradiso, ed.), Vols. I and II. Johns Hopkins Press, Baltimore, 1500 p.